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Editor Dr. Clayton M. White, Dept. of Zoology, 161 WIDB, Brigham Young University, Provo, Utah 84602

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BREEDING RESPONSES OF RAPTORS TO JACKRABBIT DENSITY IN THE EASTERN GREAT BASIN DESERT OF UTAH

by

Dwight G. Smith

Department of Biology

Southern Connecticut State College

New Haven, Connecticut 06515

and

Joseph R. Murphy

Department of Zoology

Brigham Young University

Provo, Utah 84602

Abstract

The relationships between a collective breeding raptor population of the Golden Eagle (*Aquila chrysaetos*), the Great Horned Owl (*Bubo virginianus*), the Ferruginous Hawk (*Buteo regalis*), and the Red-tailed Hawk (*Buteo jamaicensis*) and its main prey base, the black-tailed jackrabbit, is examined. By biomass, the jackrabbit is the single most important food item in the diet of each of the raptor species. Populations of each raptor species varied synchronously with jackrabbit abundance. Excepting Red-tailed Hawks, reproduction and operative breeding season mortalities were influenced by jackrabbit abundance. The role of the central Utah environment in dictating patterns of raptor response to its staple prey base is considered.

Introduction

Solomon (1949) proposed that predators respond to prey fluctuations in two distinctive ways, functionally and numerically. The functional response involves a change in food consumed by the individual predator. The numerical response involves an increase in predator density as prey increases, usually through recruitment by immigration and increased predator reproduction.

In this paper we examine the relationships between the breeding population dynamics of a collective raptor population consisting of the Golden Eagle (*Aquila chrysaetos*), the Great Horned Owl (*Bubo virginianus*), the Ferruginous Hawk (*Buteo regalis*), and the Red-tailed Hawk (*Buteo jamaicensis*) and abundance of their main prey base, the black-tailed jackrabbit (*Lepus californicus*).

The study was conducted from November 1966 through August 1970. Some additional observations were also made during the late spring and summer months of 1971 and 1972. Data similar to that which we give here are presented by Woffinden and Murphy (1977) for 1973 and 1974 for the same study area.

The exact nature of the response to changing prey densities remains unclear for many raptor species. Nicholson (1930) and Pitelka et al. (1955 a, b) have shown that tundra-inhabiting raptors exhibit strong numerical and functional responses to a cyclic and limited prey base. Responses of temperate raptor populations may be less dra-

matic. In Alberta, McInville and Keith (1974) reported that Great Horned Owls, but not Red-tailed Hawks, showed changes in breeding season density and food habits occurring synchronously with snowshoe hare (*Lepus americanus*) populations. Although Craighead and Craighead (1956) concluded that raptor population densities in Michigan tended to remain relatively stationary, the situation elsewhere is largely unknown.

Study Area

We began long term raptor studies on a 7,700 km² portion of the eastern Great Basin Desert in winter 1966. Initial studies in 1966–1968 focused primarily on Golden Eagles, Great Horned Owls, and Ferruginous Hawks (Murphy et al. 1969). Additional information on these and the Red-tailed Hawk was presented in a four-year collective raptor study on a smaller, 207 km² intensive study area (Smith and Murphy 1973). Herein we analyze raptor-jackrabbit relationships on a 1,170 km² portion of the original study area.

Topographically, the area is characterized by broad, flat alkaline valleys separated by high, north-south running ridges and hills. Valley elevations range from 1,460 to 1,620 m, and maximum elevations of the ridges and hills range from 1,830 m to upwards of 2,440 m.

Climatically the area is characterized as a northern cold desert (Shelford 1963). Annual precipitation averages 38 cm, and mean monthly temperatures range from -5°C in January to 24°C in July with wide daily and seasonal variations.

Two distinctive vegetation associations occur, the mountain desert shrub community and the dwarf conifer community. The desert shrub community is present over the lower elevations and on the valley floors. It consists of mixtures of shrubs, herbs, and grasses, several of which may, under certain edaphic soil conditions, form large communities. Two predominant shrub communities thus formed include big sagebrush (*Artemisia tridentata*) on the better drained soils, and greasewood (*Sarcobatus vermiculatus*) on the poorly drained valley floors. The well-drained slopes and hills support a dwarf conifer community of Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*) which occur in stands of widely varying density.

This part of the Great Basin has a history of chronic livestock over-grazing which dates from the late 1800s. This circumstance coupled with extensive state and federal predator-control programs, has produced conditions which allowed jackrabbit populations to drastically increase periodically to the point at which they are considered a major range pest species (Stoddard et al. 1975).

Methods

Jackrabbit Populations. We determined jackrabbit abundance by (1) transect counts, (2) road kill counts, and (3) queries of local ranchers and stockmen.

Permanent linear transects, each 805 m in length, were marked off through six large desert scrub communities, selected at random in the study area. Vegetation of the transects included typical predominant vegetation of the study area. At biweekly intervals from mid-December through March all transects were walked by two observers spaced 20 m apart. Counts derived from transects are indications of relative abundance rather than absolute population counts and reflect the basic weakness of the transect method (Southwood 1966). They do, however, provide adequate indices of population change (Gross et al. 1974) and were the only practicable means of esti-

mating jackrabbit population abundance over our large study area.

Each year we recorded winter monthly tallies of the number of local kills observed on nearby highways. Such a tally is a rough but useful index, especially when used in conjunction with other methods.

Each year we asked resident ranchers and stockmen and itinerant hunters to estimate and compare jackrabbit abundance with previous years. This questioning provided subjective information which may at the very least indicate high and low years of jackrabbit abundance.

Raptor Populations. From November 1966 through August 1970 we visited the study area at least once and usually two or more times per week to obtain information on raptor population dynamics. The 207 km² intensive study area was divided into subsections, each approximately 1.6 km², to facilitate survey. These were systematically searched in a rotating sequence for raptor nesting pairs, nonnesting pairs, and individuals at biweekly intervals beginning in mid-December and lasting through mid-May of each year.

Foot searches were supplemented by aerial surveys, but the latter were of limited usefulness because of minimum speed and altitude requirements.

Status of nesting pairs, nonnesting pairs, and single birds on the intensive study area was checked at least twice weekly during the nesting season and once weekly on the 1,170 km² study area. Throughout the four breeding seasons the single exceptional time interval between successive study area visits was 13 days in April 1970.

Raptor Food Habits. Food habits of each raptor species were determined by weekly tabulations of prey items and analysis of pellets gathered from the nest site. Prey remains were usually left on the nest, after being marked by toe clipping to avoid duplication in tabulation.

Results

Jackrabbit Populations. Jackrabbit numbers were low in 1967 and 1970, intermediate in 1968, and high in 1969 (fig. 1). The average number of individuals per transect count each year were: 1967, 3.3 ± 0.7 (range 0–7 individuals); 1968, 9.03 ± 1.2 (ranges 3–17); 1969, 13.8 ± 1.5 (ranges 6–31); and 1970, 3.6 ± 1.0 (ranges 0–9). Winter road kill counts in terms of individuals per mile of road travelled for each of the study years are: 0.8 in 1967; 1.4 in 1968; 1.9 in 1969; and 1.1 in 1970.

Subjective observations by local stockmen, ranchers, and sportsmen familiar with the study area also suggest that jackrabbit populations peaked in 1969 and declined in 1970. Our own data plus casual observations indicate that jackrabbit abundance peaked in 1969 and declined in 1970. In 1969, for example, we commonly were able to observe concentrations of 50–75 individuals feeding in small open fields of 3–5 acres during the late evening hours after sunset.

While none of these results provide conclusive evidence of jackrabbit population fluctuations, they do, considered together, strongly suggest that populations of 1968 and 1969 were considerably larger than populations of 1967 and 1970. Gross et al. (1974) conducted a separate study of jackrabbit populations approximately 200 km north of our study area. Their estimates of jackrabbit densities as determined by transects and drive counts, show a similar population low in 1967 followed by increasing population densities in 1968 and 1969. They did not find a corresponding decline in 1970 but did observe that synchrony of intermountain valley populations were in some instances 1–2 years out of phase with one another.

Avian Predator Food Habits. We have previously described the food habits of each of the avian predators (Murphy et al. 1969, Smith and Murphy 1973, and in press) and herein present only brief summaries (table 1). On a weight basis the black-tailed jackrabbit was the single most important prey item of each raptor species, contributing from a minimum of 81.6% to a maximum of 94.1% of the prey biomass con-

Table 1. Abridged food habits summaries of breeding raptors, 1967-1970.

	1967			1968			1969			1970		
	% No.	% Biomass ¹	% No.	% No.	% Biomass	% No.	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass
Golden Eagle												
<i>Lepus californicus</i>	64.0	88.8	82.0	82.0	94.1	76.8	90.7	81.1	52.5	81.1		
<i>Sylvilagus</i> sp.	17.3	10.5	11.3	5.6	5.6	17.8	9.2	17.4	25.9	17.4		
Other Mammals	14.7	0.5	5.3	0.2	0.2	4.6	0.1	0.8	19.4	0.8		
Birds	4.0	0.2	1.5	tr ³	tr ³	0.8	tr	0.7	2.1	0.7		
Totals ²	75	124360	87	266320	469375	241	469375	206945	139	206945		
Great Horned Owl												
<i>Lepus californicus</i>	23.3	81.6	42.4	89.4	66.1	66.1	90.2	87.0	47.5	87.0		
<i>Sylvilagus</i> sp.	9.3	12.3	8.2	7.6	14.6	8.7	13.7	10.9	13.7	10.9		
<i>Dipodomys</i> sp.	43.0	3.8	35.3	2.2	7.3	7.3	0.3	1.0	18.6	1.0		
Other Mammals	18.6	1.5	12.9	0.7	7.3	0.3	0.3	0.7	15.3	0.7		
Birds	5.8	0.7	1.2	0.2	4.7	0.2	0.2	0.4	4.9	0.4		
Totals	86	64789	85	92605	530711	316	530711	229813	183	229813		
Ferruginous Hawk												
<i>Lepus californicus</i>	42.0	93.7	38.6	92.3	52.4	52.4	94.0	92.2	50.0	92.2		
<i>Sylvilagus</i> sp.	2.7	2.6	2.8	2.9	4.1	4.1	3.3	5.4	6.7	5.4		
<i>Dipodomys</i> sp.	32.1	2.2	35.8	2.5	18.2	18.2	0.9	20.1	20.1	1.1		
Other Mammals	11.5	1.3	15.3	1.7	14.3	14.3	1.3	12.0	12.0	0.7		
Birds	5.4	0.1	6.4	0.3	9.1	9.1	0.2	9.2	9.2	0.2		
Reptiles	6.3	0.1	1.1	0.3	1.9	1.9	0.3	2.0	2.0	0.4		
Totals	112	115366	285	273971	393757	307	393757	242080	194	242080		
Red-tailed Hawk												
<i>Lepus californicus</i>	39.7	87.9	43.4	88.6	56.1	56.1	92.3	89.2	41.3	89.2		
<i>Sylvilagus</i> sp.	9.0	8.6	10.1	8.9	8.5	8.5	6.1	7.9	8.4	7.9		
Other Mammals	42.3	2.5	30.2	1.6	25.9	25.9	1.1	2.2	39.7	2.2		
Birds	6.4	0.7	14.7	0.8	6.6	6.6	0.2	8.9	8.9	0.4		
Reptiles	2.6	0.3	1.6	0.2	2.8	2.8	0.3	1.7	1.7	0.3		
Totals	78	81090	129	145410	296660	212	296660	190740	179	190740		

¹Weight in grams from Smith and Murphy (1973).
²Weight in grams from Smith and Murphy (1973).
³tr = trace, less than 0.1 percent.

sumed. This finding supports the contention of Clark (1972) that jackrabbits form a major part of the food base of the northern cold desert ecosystem.

On a percent frequency basis, however, some differences in prey species occurrence are evident between high prey years (1968 and 1969) and low years (1967 and 1970). Chi-square tests of the frequency of occurrence of each of the prey categories reveal significant statistical differences between years ($P < 0.01$) in Ferruginous Hawk and Red-tailed Hawk food but not for that of Great Horned Owls or Golden Eagles, although the two latter raptor species exhibit some diet differences. These differences in food between high- and low-jackrabbit years suggest a shift to alternate or buffer prey species. The observed degree of shift to alternate species was, however, not commensurate with the decline in jackrabbit abundance, and this prey species still comprised 82% or more of the food biomass of each raptor species even in low-jackrabbit years.

We believe that the abundance of jackrabbits is thus an important limiting factor which largely determines annual changes in the size and reproductive performance of the collective raptor breeding population.

Avian Predator Populations. A summary of yearly raptor population trends is presented in table 2. The annual breeding-season populations of the four species were approximately, in order of most to least common: *Buteo regalis*, *Bubo virginianus*, *Aquila chrysaetos*, *Buteo jamaicensis*. Each year pairs of another large raptor, the Swainson's Hawk (*Buteo swainsoni*), were consistently present on the study area, but were too few in number to permit detailed analysis.

The correlation between the raptor population and jackrabbit abundance is readily evident and may be categorized as the first component of numerical response. Total numbers of raptors in low-jackrabbit years varied from 18–49% below populations of high-jackrabbit years. The magnitude of change is illustrated by 1967 (a low year) and 1969 (a peak year) populations, in which almost twice as many raptors were found on the study area.

Populations of Golden Eagles and Great Horned Owls, both permanent residents, showed comparatively less yearly variation than the migratory Ferruginous Hawk and Red-tailed Hawk populations. Thus, after an initial increase from 1967 to 1968, Golden Eagle numbers varied only by 3 and Great Horned Owl numbers by 4 during the three years, 1968–1970. In contrast Ferruginous Hawk numbers changed considerably over the four-year period, with the 1969 population about one-third larger than 1968 and about twice as large as 1967 and 1970 populations. The observed recruitment of Ferruginous Hawks is probably to some extent a function of its migratory status. Studies by Craighead (1959), Naumou (1948), Galushin (1974), and others have noted the ability of several nomadic avian predator species to concentrate rapidly in areas of prey abundance. Pitelka et al. (1955 a, b) reported large variations in the highly mobile raptor populations of the Arctic tundra, and Linkola and Myllymaki (1969) observed invasions of certain raptor species during high-rodent years in Finland. Comparatively, the strongly territorial and permanently resident Tawny Owl (*Strix aluco*) was noted by Southern (1970) to maintain relatively stable numbers from year to year on his Wytham Wood Study Area in England.

Breeding Fraction of the Avian Predator Population. The tendency of pairs to breed or refrain from breeding may be considered as a part of the second component of nu-

Table 2. Raptor population trends in central Utah, 1967-1970.

Raptor Species	1967	1968	1969	1970
Golden Eagle				
No. pairs	9	14	14	13
No. breeding pairs	7	13	13	11
No. single birds	1	1	1	0
Total no.	19	29	29	26
Great Horned Owl				
No. pairs	7	16	16	13
No. breeding pairs	6	14	16	10
No. single birds	2	1	1	3
Total no.	16	33	33	29
Ferruginous Hawk				
No. pairs	19	31	38	20
No. breeding pairs	15	28	34	13
No. single birds	5	1	2	4
Total no.	43	63	78	44
Red-tailed Hawk				
No. pairs	8	12	13	12
No. breeding pairs	5	10	12	11
No. single birds	1	0	1	0
Total no.	17	24	27	24
Totals (All Species)				
No. pairs	43	73	81	58
No. breeding pairs	33	65	76	45
No. single birds	9	4	5	7
Total no.	95	149	167	123

merical response, which includes all strategies directed towards increasing predator population growth. We classified a pair as breeding if a nest was constructed and attended. For the collective raptor population, the ratio of breeding pairs to total pairs varied synchronously with jackrabbit abundance. Percentage ratios (pairs breeding to total pairs present) were 76.7% and 77.6% for the low-jackrabbit years of 1967 and 1970 respectively, 89.0% for the intermediate year 1968, and 93.8% for the peak-jackrabbit year of 1969. Only one species did not follow this pattern: the number of Red-tailed Hawk breeding pairs in 1970 was one larger than in 1968, although lower than in 1969.

In studies elsewhere, Hamerstrom (1969), Pitelka et al. (1955 a, b), and Rusch et al.

(1972) all reported increased percentages of breeding pairs of raptors during high-prey years, which contrasted sharply with a low intensity of nesting efforts in low-prey years. Southern (1970) found that the percentage of Tawny Owl pairs which each year attempted to breed varied from zero in unfavorable years to 87% in high-rodent years. He further observed that the most common way in which Tawny Owl pairs reacted to low prey was by refraining altogether from breeding.

Pairs which have constructed and attended a nest may lay their eggs or, conversely, refrain from depositing eggs and subsequently desert the nest. We did find a slightly higher incidence of nest desertion in low prey years, but unfortunately the question of possible human interference, not uncommon in our study area, renders analysis of this relationship unclear. It is quite possible, however, that pairs attempting to breed in times of low prey are more intolerant of disturbance. In favorable years breeding pairs appeared to be far more tolerant of our activities in the vicinity of the nest site (cf. Woffinden 1975 for data on this aspect).

Clutch Size. Mean clutch size of Golden Eagles, Great Horned Owls, and Ferruginous Hawks, but not Red-tailed Hawks, varied in synchrony with rodent density (table 3). Clutches of Golden Eagles varied from 1.9 in low years to 2.2 in peak years. The 1968 and 1969 clutches of Great Horned Owls and Ferruginous Hawks tended to contain a minimum of one additional egg as compared to 1967 and 1970 clutches ($t=2.58$; 2.75 respectively, $P<0.05$ for both), but not significantly different from one another ($t=1.26$; $P>0.05$). In addition, mean clutch size of 1967 and 1970 did not differ significantly ($t=1.15$; $P>0.05$). Similarly Ferruginous Hawk clutches of 1968 and 1969 were significantly larger than 1967 and 1970 clutches ($t=2.56$; 2.92 respectively; $P<0.05$) but not different from one another ($t=0.11$; $P>0.05$). Again, clutches of 1967 and 1970 did not differ significantly ($t=0.11$; $P>0.05$).

McInville and Keith (1974) found a significant increase in Great Horned Owl clutch size during years of high snowshoe hare abundance, and Houston (1971) determined that the largest brood sizes of this nocturnal avian predator coincided with years in which its prey was most abundant.

Unlike the other raptor species, clutch size of Red-tailed Hawks consistently increased each year, from a low of 2.5 in 1967 to a high of 3.3 in 1970. In contrast, McInville and Keith (1974) found that peak clutch size of Red-tailed Hawks near Alberta did occur simultaneously with highest annual snowshoe hare abundance.

For three of the four species the combination of increased numbers of breeding pairs and large clutches resulted in a greater total productivity of eggs in years of jackrabbit abundance. Correlation tests reveal a significant relationship between prey abundance and total egg production of Great Horned Owls ($r=0.97$; $t=5.24$; $P<0.05$) and Ferruginous Hawks ($r=1.98$; $t=6.64$; $P<0.05$). Total egg production of Golden Eagles and Red-tailed Hawks was slightly greater in 1968 and 1969, but the relationships are not significant ($P>0.05$ for both species).

Fledged Brood Rates. Reproductive success as measured by fledged brood rates varied considerably among the raptor species. A clear correlation between total number of fledged young, nesting success (percentage of young fledged per eggs laid), and jackrabbit abundance can be observed only for Ferruginous Hawk populations. Great Horned Owl fledged brood rates were considerably higher in favorable years, but percentage breeding success was lower in those years. To complicate the problem, the fledged brood production of Red-tailed Hawks was generally higher in favorable years, despite the increased clutch size in 1970, which was offset by increased morta-

lity of young in the nest. A major factor contributing to greatly fluctuating mortality rates from hatching to fledging is the comparatively high level of human disturbance affecting many avian predator pairs on our study area. Golden Eagles, the largest and most conspicuous of the diurnal raptors, were frequently the object of such activities as egg collecting, photography of young, deliberate nest destruction, and attempts by hunters to kill the adults. These disturbances, of course, render any analysis of yearly breeding success unrealistic unless their effect on the behavior of the birds can be resolved.

Table 3. Reproduction of large raptors in central Utah, 1967-1970.

Raptor Species	1967	1968	1969	1970
Golden Eagle				
No. clutches produced	7	13	13	11
Av. clutch size	1.9	2.0	2.2	1.9
Total eggs produced	13	26	27	21
No. nests hatching young	5	12	10	10
No. young hatched/nest	1.2	1.2	1.2	1.8
Total young hatched ¹	6 (46.2)	15 (57.7)	11 (40.7)	18 (85.7)
No. nests fledging young	5	11	9	10
No. young fledged/nest	0.8	0.9	1.0	1.7
Total young fledged ²	4 (30.8)	10 (38.5)	9 (33.3)	17 (81.0)
Great Horned Owl				
No. clutches produced	6	13	15	10
Av. clutch size	2.0	2.9*	3.3**	2.4
Total eggs produced	12	38	50	23
No. nests hatching young	5	12	14	8
No. young hatched/nest	1.8	2.5	2.7	2.3
Total young hatched	9 (75.0)	30 (78.9)	38 (76.0)	19 (82.6)
No. nests fledging young	5	11	13	8
No. young fledged/nest	1.8	1.9	2.4	1.8
Total young fledged	9 (75.0)	21 (55.3)	31 (62.0)	15 (65.2)
Ferruginous Hawk				
No. clutches produced	14	28	34	12
Av. clutch size	2.5	3.7**	3.8**	2.9
Total eggs produced	36	104	129	35
No. nests hatching young	11	25	32	9
No. young hatched/nest	1.3	2.4	3.1	1.4
Total young hatched	15 (41.7)	60 (57.7)	99 (76.7)	17 (48.6)
No. nests fledging young	10	25	31	7
Total young fledged/nest	1.2	2.2	2.9	1.4
Total young fledged	12 (33.3)	55 (52.9)	90 (69.8)	10 (28.6)

Red-tailed Hawk

No. clutches produced	5	10	12	11
Av. clutch size	2.5	2.8	3.1	3.3
Total eggs produced	13	28	37	36
No. nests hatching young	5	9	11	11
No. young hatched/nest	1.8	2.3	2.5	2.3
Total young hatched	9 (69.2)	21 (75.0)	28 (80.0)	26 (72.2)
No. nests fledging young	5	9	10	9
No. young fledged/nest	1.5	1.6	2.2	1.5
Total young fledged	8 (61.9)	15 (53.6)	22 (59.5)	14 (38.9)

^aFigures in parentheses are percentages of total eggs hatched to total eggs laid.

^bFigures in parentheses are percentages of total young fledged per total eggs laid.

*Significant at P<level.

**Significant at the P<0.01 level.

Discussion

Breeding Mortality and Regulation of Avian Predator Populations. If we arbitrarily allow that the maximum reproductive potential of the collective raptor population (excepting Red-tailed Hawks) was achieved during the peak prey year of 1969, then we may comparatively measure the limiting effects of declining prey populations on raptor reproduction. Several factors decreased breeding productivity during unfavorable years (or conversely, increased mortality). Among these were: (1) failure of pairs to nest, (2) failure of pairs to achieve maximum clutch size, and (3) failure to hatch brood, and fledge a maximum number of young. These mortality factors are related in sequential fashion. Thus, for a breeding avian predator population to have a productive year there must be a certain minimum prey density which provides the stimulus and physiological ability to breed. Further increases in prey density may be reflected in increased productivity, up to the point at which other resources may become limiting. Conversely, lower prey densities inhibit breeding and increase the probability of mortality at all breeding stages.

Southern (1970) has shown that the relationships between breeding mortalities and prey abundance may be examined by key factor analysis. This technique, developed by Varley and Gradwell (1960) and critically discussed by Ito (1972), permits inspection of the contribution of each mortality (k_i) to the total mortality (K) acting on the population.

We confined our key factor analysis to the sequence of mortality operating on the following phases of the breeding population:

- (1) k_1 = logarithm of maximum eggs producible by maximum-sized breeding population—logarithm of the number of eggs produced by the actual-sized breeding population.

The maximum breeding season population of each avian predator species was attained in 1969, and k_1 measures the mortality increase in other years when the respective species did not achieve the 1969 breeding population level. In effect, k_1 is a measure of the mortality produced by a pair's decision to breed or forgo breeding, which we believe, will be a function of available food resources.

- (2) k_2 = logarithm of eggs produced with all breeding pairs achieving maximum average clutch size—logarithm of actual number of eggs produced by breeding pairs.

The yearly average clutch size is measured against the maximum yearly average clutch size achieved. Three species attained a maximum in 1969: Golden Eagle, 2.2; Great Horned Owl, 3.3; Ferruginous Hawk, 3.8. Red-tailed Hawk maximum average clutchsize of 3.3 occurred in 1970; it was 3.1 in 1969.

(3) $k3$ = logarithm of eggs actually laid—logarithm of eggs which subsequently do hatch

This key factor measures the mortality caused by the proportion of eggs laid which do not hatch, regardless of specific cause.

(4) $k4$ = logarithm of the number of young which hatch—logarithm of the number of young which fledge.

This mortality factor measures the impact of loss of young which have actually hatched but for whatever reason do not fledge.

(5) $K = k1 + k2 + k3 + k4$

K will thus represent the absolute impact of the four stages of mortality which occur during the nesting sequence.

Results of key factor analysis for each raptor species are presented in figure 2. Although key factors are occasionally subjected to statistical treatment, Eberhardt (1970), Ito (1972), and Kuno (1973) have all suggested defects of regression analysis which may distort and invalidate results. We support their conclusions and restricted our analysis to graphical inspection, similar to that of Varley and Gradwell (1960).

Inspection suggests that the two most important mortality factors operative on Great Horned Owl populations are $K1$, the failure of a maximum number of pairs to nest, and $k2$, the failure of nesting pairs to achieve maximum clutch size. The graph of $k4$, the mortality of hatched young, diverges synchronously from K and suggests that $k1$ and $k2$ mortalities are at least partly compensated by increased survival of young in poor prey years.

Mortality factors $k1$ through $k3$ are equally additive in impact on Ferruginous Hawk reproduction. Factor $k4$ also follows K, albeit weakly. The close graphical correlation of $k1$ – $k4$ mortality factors with K suggests that Ferruginous Hawk reproduction is strongly influenced in a density-dependent manner by jackrabbit abundance.

Graphs of key factors operative on Golden Eagle populations are less readily interpreted. Although failure of maximum pairs to nest plus achieve maximum clutch size was contributory, $k3$, the failure of eggs to hatch, was the single most important mortality factor. Unfortunately, the previously discussed high level of human disturbance of Golden Eagle nests may have contributed to the importance of this mortality factor.

Graphs of Red-tailed Hawk $k1$, $k2$, and $k4$ factors partially paralleled K, suggesting that Red-tailed Hawks may have partially adjusted their reproduction to jackrabbit abundance in density-dependence fashion. The $k3$ mortality partially diverges in compensatory fashion. The overall relationships between Red-tailed Hawk reproduction and jackrabbit abundance, however, remain unclear. Red-tailed Hawk food habits during low prey years did show a higher utilization of alternate prey species as compared to the other large raptors (table 1), and it is possible that this usage of other prey was fully commensurate with jackrabbit decline.

Nature of the Predator-Prey Relationship. The nature of the relationship between the large avian predators and their stable prey base in central Utah warrants further consideration. Luttich et al. (1970) have suggested that regional raptor populations

may exhibit different adjustment patterns to a fluctuating prey base. They note that the staple prey base of the North is limited to just a few species of highly cyclic microtine rodents that Arctic raptors tend to concentrate upon and effectively exploit. They compare this response to temperate-zone raptors, which maintain notably stationary local populations, despite fluctuating prey abundance, and instead vary reproduction with prey abundance.

The large raptor populations of central Utah appear to combine elements of both response patterns. Thus, populations of each raptor species increased in high-jackrabbit years and decreased in low-jackrabbit years, suggesting that even the permanently resident populations of Golden Eagle and Great Horned Owls are in fact able to shift into an area of prey abundance. In central Utah, this ability to concentrate upon and exploit local prey abundance is most dramatically illustrated by the migratory Ferruginous Hawk populations. However, unlike northern raptor populations, which may entirely desert a locality in low-prey years, breeding populations of each large raptor species were present even during unfavorable prey years in central Utah. In these instances, the response patterns of the nesting raptors are similar to the reproductive responses revealed by other studies of temperate raptor populations, with each raptor species increasing reproductive efforts in favorable prey years.

The response patterns of the central Utah breeding raptor populations may reflect the unique nature of the disturbed habitat. The dual environmental impact of overgrazing and predator control programs have produced a comparatively simplistic food web, characterized by the superabundance of a single prey species, the black-tailed jackrabbit, which exhibits strong fluctuations in density. This results in a local desert environment which in some respects resembles the northern tundra ecosystem, and which may in turn produce the raptor breeding responses discussed in this paper.

Summary

In the years 1966–1971 we studied the relationships between a collective breeding raptor population of Golden Eagles, Great Horned Owls, Ferruginous Hawks, and Red-tailed Hawks and its staple prey base, the black-tailed jackrabbit, in central Utah.

Densities of jackrabbits fluctuate widely in this area. Each raptor species responded functionally to these jackrabbit fluctuations, consuming proportionally greater amounts of this prey species in years of higher abundance. Each raptor species also responded numerically to jackrabbit fluctuations.

Two forms of numerical responses were observed: increased concentrations of raptors in favorable years, and increased reproductive efforts of breeding raptor populations, which also varied synchronously with jackrabbit abundance. Key factor analysis of raptor species densities suggest two major reproductive strategies, the tendency of pairs to breed in favorable years and refrain from breeding in low prey years, and a variation of clutch size, with maximum clutch size produced synchronously with jackrabbit density highs.

The relationship of the raptor species populations with their chief prey base is revealed by response patterns similar in respects to both North and temperate zone raptor populations, and may reflect the disturbed nature of the central Utah habitat.

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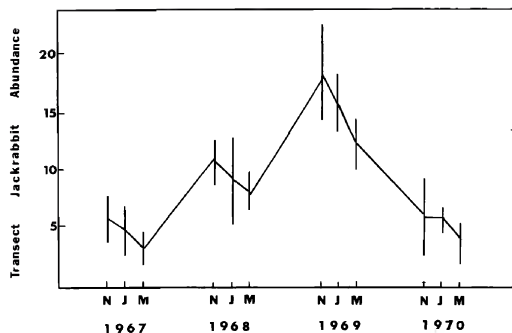


Figure 1. Transect counts of jackrabbit abundance on the central Utah study area, 1967-1970. Months presented for each year are November (N), January (J) and March (M). Vertical lines represent one standard deviation above and below average count.

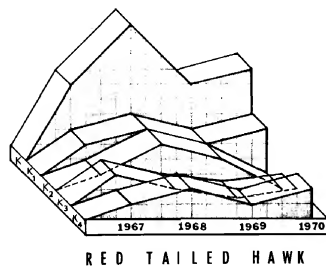
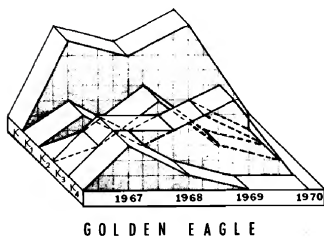
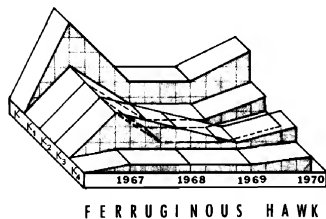
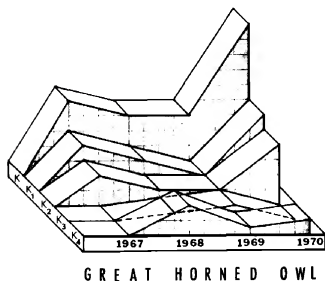


Figure 2. Graphs of key factor analysis for reproduction data of each large raptor species population on the intensive study area in central Utah, 1967-1970. Individual key factors as presented in text.

THE EGGS OF THE BLACK HAWK-EAGLE

by

Lloyd F. Kiff

Western Foundation of Vertebrate Zoology

1100 Glendon Avenue

Los Angeles, California 90024

There appears to be no published account of the eggs of the Black Hawk-Eagle (*Spizaetus tyrannus*). Therefore, it seems worthwhile to place on record the descriptions of four infertile eggs recently laid by two females of this species in the Los Angeles Zoo. The birds were obtained by the zoo in approximately 1968 and were probably captured in Ecuador (Frank Todd pers. comm.). The eggs are now in the collection of the Western Foundation of Vertebrate Zoology (WVZ).

On 5 February 1978 one female laid an egg (WVZ 42,004) which is white with heavy scallop-shaped markings and splotches of reddish-brown on the large end and a dense sprinkling of fine reddish-brown streaks and dots over the remainder of the surface. The egg is short oval in shape (Preston in Palmer, *Handbook of North American birds*, vol. 1, Yale Univ. Press, New Haven, 1962), and not glossy, and it measures 57.42×47.18 mm. The empty dry shell weight is 5.222 g.

The same bird laid another egg on 10 March 1978, or 34 days after the first egg. The second egg (WVZ 42,005) does not differ markedly from the first in color, shape, or texture, and it measures 58.06×48.06 mm. It weighed 73.522 g on 11 March before preparation, and the empty dry shell weight is 5.699 g.

The other female laid single eggs on 7 February and 10 March 1978, or 32 days apart. The 7 February egg (WVZ 42,007) is white with heavy smudges of reddish-brown towards the small end and sparse scrawls and dots of reddish-brown over the rest of the surface. The egg is subelliptical (Preston in Palmer op. cit.), and not glossy, and it bears two small calcareous tubercles on the large end. It measures 62.28×48.86 mm with an empty dry shell weight of 7.356 g.

The 10 March egg (WVZ 42,006) laid by this female is similar in most details to her first egg, except that the pattern of superficial markings is reversed with the heavy reddish-brown smudges being located nearer the large end than the small end. The egg measures 63.44×48.65 mm, and had a whole weight of 81.551 g on 11 March. The empty dry shell weight is 6.050 g.

The laying schedule of these captive birds suggests a clutch size of one, as is the case for several Old World species of *Spizaetus* (Brown and Amadon, *Hawks, Eagles, and Falcons of the World*, vol. 2, New York, McGraw-Hill, 1968). However, a Black Hawk-Eagle nest observed by Smith (1970, *Condor* 72:247-248) in Panama in 1965 and 1968 contained two young in both years.

I am very grateful to Michael Cunningham of the Los Angeles Zoo for making these eggs available for study, to Ed Harrison for preparation of the specimens, and to Michael Morrison for his assistance in various ways.

PRAIRIE FALCON CARRIES STICK TO NEST

by

John C. Barber

Division of Birds

Room E-607 NHB

Smithsonian Institution

Washington, D.C. 20560

On 27 March 1976, I watched a male Prairie Falcon (*Falco mexicanus*) carry a stick in its talons during a 91-meter (300-foot) flight from a cliff and across a canyon to a nest scrape on a ledge in Aravaipa Canyon, Graham County, 16 km (10 mi.) west of Klondyke, Arizona. The nest scrape was on a cliff facing due east, in a small pothole under an overhang, approximately 12 meters (40 feet) from the top of the cliff and 46 meters (150 feet) from its bottom. The stick was approximately 20 cm (8") long and 13 mm ($\frac{1}{2}$ ") in diameter, and was deposited on the nest ledge. The male flew off the ledge without the stick about 15 seconds after its arrival. The male was silent during the flight to and from the nest site. The female was perched above and to the south of the scrape and did not react with any movements or vocalizations to the male's behavior.

Judging by the timing of two other nests in this canyon, the incident occurred two or three days before the first egg would have been laid. The scrape was deserted before June 1, for unknown reasons. I could not recover the stick because of the degree of overhang and the steepness of the cliff.

The literature does not contain any previous record of such behavior. Nest-building in the larger falcons has not been recorded in the field with the exception of several undocumented cases (cf. Brown and Amadon, 1968, *Hawks, Eagles, and Falcons of the World*, McGraw-Hill, New York, pp. 839 and 842). Amadon (pers. comm.) has reaffirmed his earlier statement (p. 839 above) that the larger falcons probably do not build their own nests. The idea that the male may have flown with the stick in reaction to me is unlikely as I was hidden during the entire flight. Other Falconiformes sometimes bring sticks to the nest while the female is incubating, instead of bringing food, as reported by Schnell for the Goshawk (*Condor* 60:382) and Barber and Schnell for the Mexican Black Hawk (unpublished observations), but at this time the female was not incubating.

This incident appears to be a previously unreported type of pair-bonding behavior for the Prairie Falcon, but whether or not it was unique to this individual is uncertain. The publication of this note may stimulate further discussion.

Dean Amadon, M. Ralph Browning, Frank L. Beebe, and Richard R. Olendorff made helpful comments on this note. Their help is gratefully acknowledged.

COURTSHIP OF COMMON CARACARAS IN COSTA RICA

Lawrence Kilham
Department of Microbiology
Dartmouth Medical School
Hanover, New Hampshire

Between 8 and 16 January, 1978, I studied the courtship of a pair of Common Caracaras (*Caracara cheriway*) building a nest, concealed by leaves and ca 35 m up in the top of a tree (unidentified) that grew in front of the Palo Verde station of the Organization of Tropical Studies in Guanacaste, Costa Rica. I made observations with 8 × 30 binoculars, spending 4 to 5 h per day for 9 days, aided by my wife, Jane Kilham. Although I could not tell the sexes apart at a distance, I could distinguish the male (identified at times of copulation) from the female when the two were perched close to one another (a) by his being smaller and (b) having less barring on his white breast. Behavior either not previously undescribed (Bent 1938, Brown and Amadon 1968) or described in minimal detail is presented here.

Foraging. The nest tree and all of the main perching trees of the caracaras were at the edge of a tropical dry forest bordering a marsh teeming with waterfowl. As far as I could determine all foraging was done over the marsh and mostly by the male. Of 13 items brought in, 11 were definitely, and 2 probably, birds. All of these were partially plucked or dismembered by the time I saw them. Two of the heads recovered seemed to be those of Blue-winged Teal (*Anas discors*). I could not tell whether the prey was captured alive or found dead. The diet of birds was apparently unusual. I have encountered two reports of caracaras catching live birds, one by Layne et al. (1977) for Common Caracaras catching Cattle Egrets (*Bulbulcus ibis*) and one by Myers (1978) on the catching of Southern Lapwings (*Vanellus chilensis*) by the Crested Caracara (*Polyborus plan-cus*).

A neighboring pair of caracaras inhabiting a dry cattle pasture were seen feeding on carrion (once an iguana and once a tree porcupine) in the manner described by Glazener (1964) for Common Caracaras in Texas.

Transfer of prey. The female caracara began making "wuck" vocalizations on 15 January when the male, carrying the carcass of a bird in his beak, came from the marsh to the tree where she was perching. The female walked along the large limb where the two perched and took half the prey from him. Both birds then fed by holding the prey down with one foot. When the female finished, she took the remains from her mate. After a few minutes the male walked over and took part of this back again. When the female had finished her second portion, she again took the male's portion. The male yielded his portion to her three times without overt signs of being disturbed. On four of the five occasions when I saw the female feeding, it was when she took the prey from the male in this manner. On the fifth occasion the male flew with a portion of a carcass to the large, nearly horizontal limb where his mate was standing and immediately walked over to give the prey to her. Then, as she stood with head lowered and the prey in her beak, he mounted in an incomplete copulation.

Taking prey remains to the nest. On seven occasions the caracaras brought prey remains, which consisted of nothing but bones and tendons, to the nest. On five of these

the bird bringing the debris waited 13 to 20 min before its partner left, whereupon it deposited the material.

Presumably the remains were being used to line the nest, for the caracaras were also bringing in sticks at this time. I could not reach the nest because the branches at the very top of the tree, where the nest was located, were too small for climbing.

Perching and allopreening. The caracaras, especially the female, spent much of each day perching in trees overlooking the marsh. I saw the pair allopreen 6 times. The events on 16 January were representative. The female had finished feeding. Shortly thereafter the male finished, and he approached the female and perched within a few inches of her. When she put her head down, he nibbled at the feathers of her crown. After both birds had preened individually for a few minutes, the male presented the side of his neck and she nibbled at it. More individual preening ended when she again put her head down for him to preen. The male had thus preened the female twice to her once, a consistency shown in other sessions. The two caracaras, when resting and preening, often perched within 30 cm of each other.

Copulatory behavior. I witnessed four incomplete copulations—two on the limb where the pair fed, one on a small tree top in the marsh, and one (not well seen) on the nest. In three of the four the male alighted on the back of the female without preliminaries, staying on for about 4 seconds. In the fourth episode the male first presented his mate with food, then mounted while she held the prey in her beak, as described above.

Vocalizations. The only vocalizations heard were low, single "wuck" or "g-wuck" notes. The notes were given when one caracara was approaching the other, either with prey, or with debris when one partner was on the nest. Strong winds in the area made study of vocalizations difficult. I never heard the cry, described by Bent (1938) and Slud (1964) that is given from some high perch with a backward toss of the head.

Conflict. One of the pair pursued an intruding caracara on two occasions. When the intruder flew near the nest, the two caracaras with claws outstretched, beat their wings as they tried to grapple with each other in the air.

In summary, the birds did little flying other than to forage over the marsh. No display flights were observed. The birds often perched close to one another and allopreened, usually after the male had brought prey to the female and both birds had fed. There were no preliminaries to incomplete copulations in three instances but presentation of prey by the male preceded a fourth. The female assumed no consistent precopulatory pose.

Acknowledgments

I am obliged to James N. Layne and to David H. Ellis for reading and commenting on my observations.

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AN OBSERVATION OF THE AERIAL COURTSHIP OF THE RED-TAILED HAWK

by
Mark Andrew Springer
Department of Zoology
Miami University
Oxford, Ohio 45056

On April 5, 1976, while in an observation blind 35 feet from a Red-tailed Hawk nest at Alum Creek Reservoir in Delaware County, I observed the aerial courtship of the Red-tailed Hawk (*Buteo jamaicensis*). As the pair flew into the thermals, both hawks participated in dives, barrel rolls, and ascents. While coming out of independent dives, the birds were observed to make contact with their talons. During the three-second contacts, the birds spiraled downward and then separated. Typical dives and ascents followed each of the two encounters. As the female began to return to the nest, the smaller male approached her from above. With legs and tail extended downward, he dropped down and grasped the back of the female. She responded by raising her tail. The copulation lasted about two seconds after which both birds returned to the nest tree where normal copulatory behavior commenced.

Conner (1974, *Bird Banding*, Summer Vol., p. 269) noted that the male of a pair of Red-tailed Hawks made aerial contact with its mate, but the female did not respond by lifting her tail.

CAUTION ON USING PRODUCTIVITY OR AGE RATIOS ALONE FOR POPULATION INFERENCES

by

James W. Grier, Zoology Department
North Dakota State University
Fargo, North Dakota 58105

One frequently sees published statements or hears that a population is declining because reproduction is decreasing or because age ratios are changing. Examples are easy to find; I deliberately have not singled out any specific instances here. The conclusion "declining population" might be true, but it also might not be. Such a conclusion does not necessarily follow from the observed reproductive or age-ratio changes unless other characteristics of the population, such as time-specific mortality rates, remain constant. The assumption that other population characteristics remain constant is rarely stated and may be very dangerous to the interpretation.

The points I wish to make are already known to population biologists (see, e.g., C. J. Krebs, *Ecology*, Harper and Row, 1978, ch. 9-11; and D. B. Mertz, in: J. H. Connell et al. (eds.), *Readings in Ecology and Ecological Genetics*, Harper and Row, 1970, pp. 4-17). Caughley (*J. Wildl. Manage.* 38:557-562, 1974) described the problem well: "Age ratios unsupported by other information seem to be statistics in search of an application." But the principles are not intuitive or obvious. Enough researchers, including raptor workers, are routinely trapped by them that they need to be emphasized.

To illustrate these principles I have chosen hypothetical but realistic examples using standard life-table or life-equation calculations (see Krebs, 1978, ch. 10). The computations were facilitated with a BASIC computer program (which can be used on most computers, including many small office or home models). The program is of general utility and is provided in the Appendix. Any potential users are cautioned, however, that life tables themselves can be misleading; they involve several assumptions, such as age stability and constant population characteristics. Life tables are useful for modeling, as I have done here, but they should not be used for estimating survival rates from band recoveries, a common practice in the past (see note in the program listing). The program given in the Appendix additionally assumes a constant age-specific mortality rate for all birds over one year of age and death before they reach their physiological "old-age" under normal ecological conditions.

For example proving that reproductive information alone can be misleading, consider the hypothetical situation in table 1. In population B the rate of reproduction is only one-half that of population A, but population B is *growing* at a rate of 14 percent per year while population A is decreasing at a rate of 12 percent per year! If you find that hard to believe, study the table and perhaps perform the calculations yourself. The reason for the seeming paradox is that higher survival (lower mortality) more than compensated for the lower reproduction in population B.

Table 2 illustrates the problem with age ratios. Again, one of the hypothetical populations is declining while the other is increasing, but the age ratios are identical! A researcher watching these two populations, perhaps Peregrine Falcons, passing on migration could not distinguish between them on the basis of age ratios. The increasing

population does so because higher reproduction is producing more first-year birds *and* because lowered mortality is resulting in more older birds. But the *ratio* of first-year to older birds has remained the same. The point is that age ratios are difficult, if not often impossible, to interpret. It is like, in a case of simple division, trying to determine the dividend and the divisor when only the quotient is known. Caughley (1974) provides more examples.

Age ratios in the form of "catch curves" are occasionally useful in fisheries, but even they are beset with problems. They often have the advantage of strong age-classes to help serve as markers in the population. Usually when age ratios are reliable, one does not know it unless other data are also available for comparison. But then those other data are sufficient for what one wants to know, and the age ratios are unnecessary.

Population trends can be estimated by comparing age-specific reproduction and mortality (i.e., the life-table approach) but only when both reproduction and mortality information are available or if a constant time-specific mortality rate can be assumed. The only good, clear data that I have seen in an example where reproductive changes are in fact reflected in population changes involves Paul Spitzer's Osprey data for the northeastern United States (personal communication and presentation at the 1978 RRF Annual Meeting). In addition to the presence of good data on both reproduction and the actual total size of the breeding population over a period of years, the Osprey example involves a relatively unique (for raptors) situation: a small but fairly rapidly growing population where intraspecific competition and related mortality probably have not resumed significantly. Hence the mortality rate is probably at a relatively low, constant "background" level.

In the case of Peregrine Falcons in the eastern United States (see J. J. Hickey, ed.), *Peregrine Falcon Populations*, Univ. of Wisconsin Press), reproduction dropped and the falcons disappeared. But the specific relationships between reproduction, mortality, time, and actual population changes are far from clear, and we are left with only a rough picture based on hindsight. Reproductive changes might be serious, as they apparently were for Peregrines, and we could lose a population by waiting. Or changes in reproduction might not be significant and we can make fools of ourselves and stretch credibility by rushing in and sounding alarms that are not needed. Hindsight can be painful either way. To avoid the problem of not knowing whether estimated reproductive changes are serious and having to wait for hindsight, the solution is to invest more time and effort (and money) to obtain better data for both reproduction *and* mortality. Trying to make inferences when you have only half the picture can be tricky. As a further safeguard for one's inferences, it helps to have, if possible, other measures of the population, such as proper sampling surveys and/or mark-recapture programs with adequate proportions of recaptures.

In summary, although age ratios and reproductive information occasionally might be useful if used alone, it is risky unless one has additional information (as in P. Spitzer's Osprey case) for a backup. Perhaps in the future after more clear examples consistently show that assumptions like constant time-specific mortality are reasonable, we can use age ratios and reproductive data alone with more confidence. But until then I urge that we proceed with caution.

Acknowledgments

I thank D. H. Johnson and H. Postovit for comments on earlier drafts of this ar-

ticle and P. Spitzer for discussions on his Osprey data.

Table 1. Hypothetical example of lowered reproduction in an increasing population.

	Population 1	Population 2
Average number young per successful nest	6	2
Average number young per adult	1.5	0.5
Age begin breeding	2	2
Proportion of adult females successfully breeding	50%	50%
Average number of daughters per successful female	3	1
First-year mortality	70%	35%
Annual mortality for older birds	50%	10%
ANNUAL RATE OF POPULATION CHANGE	-24%	+ 14%

Table 2. Age ratios in two hypothetical Peregrine Falcon populations.

Life Table Characteristics	Declining Population	Increasing Population
GIVEN		
First-year mortality	70%	50%
Annual mortality for older birds	25%	20%
Age begin breeding	3	3
Breeding success rate for adult females	60%	60%
Average number of daughters per successful female	1.15	1.25
CALCULATED		
Average number of young per adult	0.69	0.75
Maximum age (for an initial cohort of 1,000)	18	24
Annual rate of population change	-12%	+ 2%
Age ratios:		
first year (immature plumage)	32%	31%
over first year ("adult" plumage)	68%	69%

APPENDIX

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10 PRINT
20 PRINT "      *** AVIAN LIFE TABLE ANALYSIS ***"
30 PRINT
40 PRINT "      BY JAMES W. GRIER"
50 PRINT "      ZOOLOGY DEPT., NDSU, FARGO 58105"
60 PRINT

70 PRINT
80 PRINT "DO YOU WANT INTRODUCTORY INFRMATION (1=YES, 2=NO)";
90 INPUT A0
100 IF A0=2 THEN 310

```


CORRECTION: Table 1, page 22, Vol. 13 (1) 1979
 Grier — Caution on Population Inferences

Table 1. Hypothetical example of lowered reproduction in an increasing population

	Population A	Population B
Average number young per successful nest	4	2
Average number young per adult	1.0	0.5
Age begin breeding	2	2
Proportion of adult females successfully breeding	50%	50%
Average number of daughters per successful female	2	1
First year mortality	65%	35%
Annual mortality for older birds	35%	10%
ANNUAL RATE OF POPULATION CHANGE	-12%	+ 14%

Table 2. Age ratios in two hypothetical Peregrine Falcon populations.

Life Table Characteristics	Declining Population	Increasing Population
GIVEN		
First-year mortality	70%	50%
Annual mortality for older birds	25%	20%
Age of first breeding	3	3
Breeding success rate for adult females	60%	60%
Average number of daughters per successful female	1.15	1.35
CALCULATED		
Average number of young per adult	0.69	0.81
Annual rate of population change	-12%	+ 3.5%
Age ratios:		
first year (immature plumage)	32%	32%
over first year ("adult" plumage)	68%	68%

```

110 PRINT "THIS PROGRAM CALCULATES POPULATION GROWTH RATES AND"
120 PRINT "A NUMBER OF OTHER POPULATION CHARACTERISTICS FOR"
130 PRINT "BIRDS -- ASSUMING A CONSTANT MORTALITY RATE FOR"
140 PRINT "INDIVIDUALS OVER ONE YEAR OF AGE AND THAT THE BIRDS"
150 PRINT "DIE BEFORE REACHING THEIR PHYSIOLOGICAL LIMITS,"
160 PRINT "THAT IS, FEW BIRDS DIE IN THE WILD FROM "OLD AGE.""
170 PRINT
180 PRINT "FOR A REFERENCE FOR SOME OF THE OTHER ASSUMPTIONS,"
190 PRINT "SYMBOLS AND MATHEMATICS, SEE: C. J. KREBS."
200 PRINT "1978. ECOLOGY. HARPER AND ROW, PUBL. N.Y. CHAPTER 10."
210 PRINT
220 PRINT "CAUTION: LIFE TABLES ARE USEFUL FOR MODELING BUT THEIR"
230 PRINT "INTERPRETATION CAN BE TRICKY AND THEY SHOULD"
240 PRINT "NOT BE USED FOR ESTIMATING SURVIVAL RATES --"
250 PRINT "SEE: BROWNIE, ANDERSON, BURNHAM, AND ROBSON."
260 PRINT "1978. U.S. DEPT. OF INTERIOR, FISH & WILDLIFE"
270 PRINT "SERVICE, RESOURCE PUBL. NO. 131."
280 REM NOTE TO PERSONS READING THE PROGRAM: SOME OF THE VARIABLES
290 REM USED INTERNALLY (NOT PRINTED) MAY NOT BE THE SAME AS IN THE
300 REM TEXT. E.G., R1="R(0)" AND R2="LITTLE R".
310 PRINT
320 PRINT "WHAT SPECIES ARE YOU WORKING WITH";
330 INPUT S$
340 PRINT "NOTE: INDICATE ALL RATES OR PERCENTAGES AS PERCENTAGES."
350 PRINT "WHAT IS YOUR ESTIMATE OF THE FIRST YEAR MORTALITY"
360 PRINT "RATE FOR ";S$;"S";
370 INPUT L
380 PRINT "WHAT IS YOUR GUESS FOR THE ANNUAL MORTALITY"
390 PRINT "RATE OF OLDER BIRDS";
400 INPUT U
410 PRINT "AT WHAT AGE DO YOU BELIEVE ";S$;"S NORMALLY"
420 PRINT "BEGIN BREEDING";
430 INPUT B
440 PRINT "WHAT IS YOUR ESTIMATE OF THE PERCENTAGE OF ADULT"
450 PRINT "FEMALES THAT PRODUCE FLEDGLINGS EACH YEAR";
460 INPUT F
470 PRINT "WHAT IS THE ANNUAL AVERAGE NUMBER OF FEMALE YOUNG"
480 PRINT "RAISED BY SUCCESSFUL FEMALES (CAUTION: THINK"
490 PRINT "CAREFULLY THIS IS USUALLY OBTAINED BY DIVIDING THE"
500 PRINT "AVERAGE TOTAL NUMBER OF YOUNG PER FEMALE BY 2)";
510 INPUT Y
520 PRINT
530 DIM X(75),L(75),D(75),Q(75),S(75),M(75),W(75),A(75)
540 MAT X=ZER(75)
550 MAT L=ZER(75)
560 MAT D=ZER(75)
570 MAT Q=ZER(75)
580 MAT S=ZER(75)
590 MAT W=ZER(75)
600 MAT M=ZER(75)
610 FOR P=1 TO 75
620 LET X(P)= P-1
630 NEXT P
640 LET L(1)=1000
650 LET L(2)=INT(1000*(1-(1/100)))
660 FOR P=2 TO 75
670 LET L(P+1)=INT(L(P)*(1-(D/100)))
680 IFL(P+1)=0THEN700
690 NEXT P
700 FOR P=1 TO 75
710 LET D(P)=L(P)-L(P+1)
720 IFO(P)=0THEN740
730 NEXT P
740 FOR P=1 TO 75
750 IFL(P)=0THEN780
760 LET Q(P)=D(P)/L(P)
770 NEXT P
780 FOR P=1 TO 75
790 LET S(P)=1-Q(P)
800 IFL(P)=0THEN820
810 NEXT P
820 FOR P=1 TO 75
830 IFX(P)CUTHEN850
840 LET W(P)=(F*Y/100)*L(P)/1000
850 NEXT P
860 FOR P=1 TO 75
870 LET M(P)=X(P)*M(P)
880 IFL(P)=0THEN900

```

```

890 NEXT P
900 LET R1=0
910 LET T=0
920 FOR P=1 TO 75
930 LET R1=R1+M(P)
940 LET T=T+W(P)
950 NEXT P
960 LET G=T/R1
970 LET R2=(LOG(R1))/G
980 PRINT "M(X) FOR BREEDING ADULTS IS";F*Y/100;". "
990 PRINT "L(X) WILL START AT 1,000 BUT IT WILL BE CONSIDERED"
1000 PRINT "AS STARTING AT 1.00 FOR L(X)M(X) PURPOSES."
1010 PRINT
1020 :      #####          #####          #####          #####
1030 :      #####          #####          #####          #####
1040 PRINT "TABLE 1. LIFE TABLE FOR ";SS;"S."
1050 PRINT
1060 PRINTUSINGI020,"X","L(X)","D(X)","G(X)","S(X)","L(X)M(X)"
1070 PRINT "-----"
1080 FOR P=1 TO 75
1090 PRINTUSINGI030,X(P),L(P),D(P),G(P),S(P),M(P)
1100 IFL(P)=0THEN1120
1110 NEXT P
1120 PRINT "-----"
1130 LET T=0
1140 MAT A=ZER(75)
1150 FOR P=1 TO 75
1160 LET A(P)=(EXP((-R2)*X(P)))*M(P)
1170 LET T=T+A(P)
1180 NEXT P
1190 PRINT
1200 PRINT "TABLE 2. ESTIMATE OF INNATE CAPACITY FOR INCREASE."
1210 PRINT
1220 PRINT "X","E**(-LITTLE R*X)L(X)M(X)"
1230 PRINT
1240 FOR P=1 TO 75
1250 PRINT X(P), A(P)
1260 IFL(P)=0THEN1280
1270 NEXT P
1280 PRINT
1290 PRINT " ", "-----"
1300 PRINT "TOTAL", T
1310 PRINT
1320 PRINT "THE ESTIMATE OF THE INSTANTANEOUS RATE OF INCREASE"
1330 PRINT "{'LITTLE R'} IS";R2;". OR A FINITE ANNUAL RATE"
1340 PRINT "{'BIG R'} OF";EXP(R2);"."
1350 PRINT
1360 PRINT "ARE YOU SATISFIED WITH THIS ESTIMATE (1=YES, 2=NO)";
1370 INPUT A
1380 IF A=2 THEN 1640
1390 MAT W=ZER(75)
1400 FOR P=1 TO 75
1410 LET W(P)=[(EXP(R2))*(-(P-1))]*(L(P)/1000)
1420 IFL(P)=0THEN1440
1430 NEXT P
1440 LET T=0
1450 FOR P=1 TO 75
1460 LET T=T+W(P)
1470 NEXT P
1480 PRINT
1490 PRINT "TABLE 3. PERCENTAGE OF POPULATION IN EACH AGE CLASS."
1500 PRINT "      (THE STABLE AGE DISTRIBUTION)"
1510 PRINT
1520 PRINT "X","PERCENTAGE IN CLASS"
1530 PRINT
1540 FOR P=1 TO 75
1550 PRINT X(P), 100*(W(P)/T)
1560 IFL(P)=0THEN1610
1570 NEXT P
1580 PRINT "DO YOU WANT TO RUN ANOTHER LIFE TABLE ANALYSIS (1=YES, 2=NO)";
1590 INPUT A
1600 IF A=1 THEN 310
1610 PRINT
1620 PRINT "SEE YA"
1630 STOP
1640 PRINT "WHAT INSTANTANEOUS RATE DO YOU WANT TO TRY THIS TIME";
1650 INPUT R2
1660 GOTO1130
1670 END

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ABSTRACTS OF THESES AND DISSERTATIONS

THE BIOLOGY OF THE NEW ZEALAND FALCON

(Falco novaeseelandiae Gmelin 1788).

Morphological differences of 232 New Zealand Falcons were investigated by measuring nine parameters. Three allopatric forms occupying different habitats are recognized. These are small, dark forest-living "Bush Falcons," large, pale "Eastern Falcons" living in predominantly open montane areas, and intermediate "Southern Falcons" inhabiting Fiordland, New Zealand, and the Auckland Islands. Seventeen adaptive features of New Zealand Falcons were compared with those of congeners to investigate possible taxonomic relationships. The preliminary opinion is reached that *F. novaeseelandiae* is most closely related to *F. deiroleucos*, *F. ruficularis*, and *F. femoralis*. Eight factors which might be adaptive toward sexual dimorphism are briefly discussed, and the hypothesis was reached that the strongest selection pressure toward sexual dimorphism operates through the attacking ability of juvenile raptors, more so in those species which specialize in the attacking aspect of hunting and less so in those which specialize in the searching aspect.

The diet of Eastern Falcons was deduced by analysis of 932 pellets and 661 prey remnants, representing about 1,434 prey individuals of about 32 species captured by 30 pairs of falcons. Analyses of 21 stomachs and 68 attacks on prey by wild falcons are documented. About 80% of prey individuals (61% by biomass) were small passerines, particularly the Yellowhammer (*Emberiza citrinella*), Greenfinch (*Chloris chloris*), Skylark (*Alauda arvensis*), New Zealand Pipit (*Anthus novaeseelandiae*), and Blackbird (*Turdus merula*). About 3.2% of individuals (38% by biomass) were introduced mammals, mainly Brown Hares (*Lepus europaeus*) and European Rabbits (*Oryctolagus cuniculus*). Skinks (*Leiopeltis* sp.) and insects (16.4% of individuals) comprised only 0.8% by biomass. The dietary values of preys and the food consumption of two New Zealand Falcons were measured experimentally and used to calculate the prey requirements of a breeding pair of falcons. Data on 280 range stones from 16 pairs of wild New Zealand Falcons are given.

The hunting strategies of raptors are briefly reviewed and 7 search and 4 attack behaviors recognized and described. Thirty-eight hunts by wild New Zealand Falcons and 194 hunts by trained or semitrained (at hack) falcons are categorized. Instances of nest-robbing and food storing are described.

Methods used to find 144 nest areas in 5 study areas totalling 7,800 km² in South Island, New Zealand, and the known history of each site are given. Ninety-four nesting territories in area A and 21 in area C averaged 3.80 and 3.95 km apart. Orientations and heights of 44 roosts of 3 types, and orientations and descriptions of 42 nests of 4 types are given. Nests were found on cliff ledges, ground ledges, under logs in forest, and among epiphytes in trees. Tape recordings and sonograms of 6 calls are supplied and 19 postures or behaviors are described and illustrated. Courtship and stages of the reproductive cycle are outlined. Mean clutch size was 2.68 (mode = 3, n = 25), mean egg size was 48.7 X 36.7 mm (n = 69), mean brood size for 32 nesting attempts was 1.88 (range 0-4), for 23 successful nestings, 2.61. Incubation was about 30-32 days, recycling time about 16 days. Data on weight gains, tarsus and rectrix growth, and developmental stages of chicks are supplied. The methods and results of

a successful captive breeding project are given.

Organochlorine levels in pectoral muscles of 12 New Zealand Falcons and 14 other New Zealand birds of prey are tabulated. Five juvenile falcons contained a mean of 2.57 mg total DDT per kg wet weight of muscle, 5 adults 13.74 mg/kg. Shell-thinning since 1948 was 0-3.3% in 15 shells. The known status of New Zealand Falcons in all parts of New Zealand is given and summarized in two distribution maps. About 3,100-3,200 pairs of Eastern Falcons, 450-850 pairs of Bush Falcons and 140-270 pairs of Southern Falcons may exist. Probably 3,000-4,500 pairs of New Zealand Falcons is a realistic estimate.

Fox, Nicholas C. 1977. The biology of the New Zealand Falcon (*Falco novaeseelandiae* Gmelin 1788). Ph.D. thesis. University of Canterbury, Christchurch, New Zealand. 421pp.

ECOLOGY OF THE WHITE-TAILED KITE IN SAN DIEGO COUNTY

White-tailed Kites were studied from April 1975 to March 1978 in San Diego, California. The ecology and behavior of both breeding and nonbreeding kites were examined.

Data were obtained on nest sites, nesting success, diet, foraging activity, prey density, and communal roosting behavior.

Of 26 nests studied, 20 contained eggs (mean of 4.0 eggs per clutch) and 17 fledged young (mean of 1.9 fledglings per clutch). Four pairs produced a second clutch during the 1977 nesting season.

Territoriality existed to varying degrees. Intraspecific territoriality was uncommon yet readily visible. Two pairs of kites were evicted from their nesting territories by pairs nesting nearby. Interspecific territoriality was most commonly seen against Red-tailed and Marsh hawks. Other bird species were attacked less frequently.

In 2886 pellets analyzed, 3266 prey animals were represented. Of these 2759 (84.5%) were *Microtus californicus*, 344 (10.2%) *Reithrodontomys megalotis*, 143 (4.4%) *Mus musculus* and 30 (0.9%) other organisms. Only five birds and no reptiles or invertebrates were found in the pellets.

With use of the runway analysis technique, the relative *Microtus* population densities were determined in the kite's hunting areas for each site.

A stepwise multiple regression analysis was used to relate these variables (nest data, diet, and prey density) to number of eggs, number of hatchlings, number of fledglings, and nesting success of each nest site.

The number of eggs was related to the mean number of active *Microtus* runways (prey density) in the kites' hunting areas and to the height of the nest in the ($R^2 = 52.0\%$). Number of hatchlings were not significantly related to any of the variables. The number of fledglings, and nesting success, were related to the percent of *Microtus* in the kite's diet ($R^2 = 26.9\%$ and $R^2 = 41.1\%$ respectively). From these results it was determined that the number of eggs is related to the prey density, and the number of fledglings and nesting success are related to the percent of *Microtus* in the diet.

Communal roosting sites were observed at four locations in San Diego County. A roost at Sorrento Valley was observed at least once per week from early October, 1977 to late March, 1978. Abundant rainfall flooded the valley for most of December, 1977 and February, 1978, decimating most of the *Microtus* population. As the prey density in the valley decreased, so did the number of kites using the valley for hunting purposes and for communal roosting. I found that the kites entered and left the roost in response to conditions of visibility, which was closely related to light intensity except under foggy conditions.

Wright, Bruce Albert. 1978. Ecology of the White-tailed Kite in San Diego County. M.S. thesis. San Diego State Univ. San Diego, Calif. 60 pp. Present Address: Rt. 4 Box 4617-1, Juneau, Alaska 99803.

ECOLOGY OF WINTERING BALD EAGLES ON THE SKAGIT RIVER, WASHINGTON

Winter ecology and behavior of a Bald Eagle (*Haliaeetus leucocephalus*) wintering population were studied in the winters of 1973-74 and 1974-75. Analysis was undertaken of the distribution of the eagles along the river in relationship to the distribution and abundance of the food source. Wintering Bald Eagle habitat selection in relation to habitat availability, distribution, and human disturbance were also described. Criteria for aging sub-adult Bald Eagles in the field were substantiated through molt research on captive eagles. Plumage aging techniques were used to determine the differential arrival and departure dates of different age classes, and behavioral relationships between eagles of different ages in the wintering area. The main food source of the Skagit wintering population is dead salmon (*Oncorhynchus* spp.). Eagles were never observed to kill live salmon. Eagle numbers were correlated to the amount of available salmon. When most salmon carcasses were either washed away by river currents or consumed by eagles, the wintering population dispersed and left the area. Eagles were concentrated in a seven mile stretch of river and were further concentrated within this seven mile stretch at certain gravel bars where salmon carcasses and perching sites were abundant. The population begins to arrive in mid-October with adults arriving first. Most sub-adults arrive in early December. The eagle population peaks were 93 eagles in mid-January 1974 and 165 eagles in mid-February 1975. The lower population level in 1974 was influenced by a flood on 16 January which prematurely removed most salmon carcasses that year. The Bald Eagle population disperses from the Skagit area during March, and few eagles remain after 1 April. The average percentage of sub-adults in the population was 52.6%. This figure is higher than all other wintering sub-adult percentages except Shea's 1971 figure of 54.5% in Glacier National Park, Montana. This may indicate a healthy, productive population, however, sub-adult percentages cannot be utilized to determine population productivity until much more is known about the winter distribution and habitat selection of different age classes. Eagle activity was affected by weather conditions. High winds and clear skies stimulated soaring and flying activity. Consequently, high eagle counts occurred during calm periods with low overcast skies when most

eagles were perching along the river. During sunny, windy weather, eagles soared in groups and did not display usual feeding and distribution patterns. The social function of such group soaring is discussed. Eagles initially utilized areas on the river that were isolated from human disturbance, and only when food was depleted in these areas did the eagles use sites close to human disturbance. Of 3,322 eagle observations in 1974-75, 68.5% were on the side of the river having no road access; 19.7% were on islands in the river; and 11.8% were on the side of the river where the main road is, and most human activity occurs. Management alternatives to minimize human disturbance and preserve eagle wintering habitat are discussed.

Servheen, Christopher W. 1975. Ecology of Wintering Bald Eagles on the Skagit River, Washington. M.S. thesis, University of Washington, Seattle. 96 pp.

THE INFLUENCE OF FORCED-RENESTING ON REPRODUCTIVE PARAMETERS OF CAPTIVE AMERICAN KESTRELS

Abstract

From 1974 to 1977, the first clutches of 78 pairs of captive American Kestrels (*Falco sparverius*) were removed to induce laying of replacement clutches. This procedure was termed forced-renesting. First clutches were artificially incubated and the hatchlings hand-reared to fledging age.

A Maximum Likelihood Program revealed that replacement clutches had fewer eggs, longer eggs, and eggs with thicker shells than first clutches; but they did not differ in fertility, hatchability, overall growth, and fledging success of young. Clutch size, egg length, eggshell thickness, and fresh-egg weight declined seasonally. Hatchling weight and fresh-egg weight were highly correlated, but neither was a reliable index of growth beyond 6 days of age.

Hand-rearing was associated with slower growth rates and the production of physically smaller adults. Hand-reared females laid the largest clutches and the largest and heaviest eggs and were associated with higher fertility than hand-reared males.

The implications of forced-renesting are discussed.

Bird, David M. 1978. The influence of forced-renesting on reproductive parameters of captive American Kestrels. Ph.D. thesis, McGill University, Montreal, 111 pp.

BEHAVIORAL ECOLOGY OF RED-TAILED HAWKS (*BUTEO JAMAICENSIS*), ROUGH-LEGGED HAWKS (*B. LAGOPUS*), NORTHERN HARRIERS (*CIRCUS CYANEUS*), AMERICAN KESTRELS (*FALCO SPARVERIUS*), AND OTHER RAPTORIAL BIRDS WINTERING IN SOUTH CENTRAL OHIO

Abstract

A field study of the behavioral ecology of sympatric Red-tailed Hawks (RTH), Rough-legged Hawks (RLH), Northern Harriers (NH), American Kestrels (AK), and other raptorial birds wintering in a 73.5 km² tract in south central Ohio was conducted during the winters of 1973-74 through 1976-77.

Ten species of Falconiformes and three species of Strigiformes were seen in the area during the four winters of study. RTH, RLH, NH, and AK comprised over 99 percent of the individuals seen. The size and composition of this four-species raptor community remained remarkably constant during the four winters of study, ranging from 1.22 birds/km² in 1976-77 to 1.40 birds/km² in 1975-76.

Interspecific spatial overlap was greater in areas of high use than in areas of moderate and low use. Intraspecifically, NH showed the greatest amount of interseasonal overlap, and AK showed the least.

The four species all used cropland more than expected and grazed pastures less than expected on the basis of habitat type availability. Interspecific differences in all species pairs occurred with respect to vegetation type, field size, and field slope selected. Activity dependent shifts in vegetation type use occurred in all four species. Intraspecific differences in vegetation type use occurred in NH. The four species differed in use of fields bordered by woodlots, tree rows, or roads. RTH, RLH, and NH avoided areas within 75 m of active farmsites whereas AK preferred them. Depending on the field characteristic examined, niche breadths (J') differed considerably among the four species, and when these are viewed in conjunction with changes in the degree of niche overlap (ϕ) between species pairs for each of the field characteristics, an extremely complex pattern of niche overlap and habitat use emerges.

RLH, NH, and AK all showed significant shifts in temporal activity. While RTH, RLH, and AK did not differ from one another with respect to temporal patterning, all three species did differ significantly from NH. Significant temporal shifts in the percentage of birds flying when sighted occurred in RTH and RLH, but not in NH or AK.

Interspecific differences in the ratio of flying to perched birds occurred in all paired species comparisons. Only NH were observed more frequently flying than perched, and only NH pounced more frequently from flight than from a perch. The four species differed with respect to both perching height and perching substrates. The three tree perching species (RTH, RLH, and AK) partitioned that resource according to the height of the tree, their perching height, the location of the tree, and their perching location in the tree. The four species differed in the amount of flap-sailing, hover-flying, and soaring they engaged in, as well as the height and speed at which they flap-sailed. Harriers differed intraspecifically in the flight types they employed and in the height and speed at which they flew.

There were intraspecific differences in pouncing success and hunting bout success. Juvenile harriers were less proficient hunters than adult harriers. In all species hunting success depended on vegetation type hunted. In NH and AK hunting success depended on pounce type.

Variations in temperature, relative humidity, solar radiation, precipitation, and wind velocity were accompanied by shifts in raptor activity.

Numerically small mammals made up the bulk of RLH and NH diets, and in all species but RTH small mammals comprised the majority of the diet by biomass. RTH pirated more prey from other raptors than did the other three species. Adult male harriers took more avian prey than did adult female or unsexed juvenile harriers. The percent of insects in the diet of AK increased with increasing temperatures.

One hundred three interspecific and 69 intraspecific encounters among RTH, RLH, NH, and AK were observed. In 20 percent of the encounters, prey robbery or carcass displacement was attempted. Both RLH and NH were victims of piracy.

While overall species overlaps (ϕ) indicated a similar degree of niche overlap for all four species, RTH, NH, and AK all exhibited at least one overwhelming difference in their niche from the other three species while RLH did not. On the basis of the relative degree of overlap, activity and diet, rather than habitat, were the most important niche dimensions, and time was least important. Weather-related changes in the behavior of the four species resulted in shifts in the diversity of niche parameters that were of the same order of magnitude as interspecific differences in the same parameters. Viewed in their entirety, these data indicate considerably complex resource partitioning among the four species comprising this open-habitat raptor guild.

Bildstein, K. L. 1978. Behavioral ecology of Red-tailed Hawks (*Buteo jamaicensis*), Rough-legged Hawks (*B. lagopus*), Northern Harriers (*Circus cyaneus*), American Kestrels (*Falco sparverius*), and other raptorial birds wintering in south central Ohio. Ph.D. dissertation. The Ohio State University, Columbus. 364 pp.

Present address: Keith L. Bildstein
Department of Biology
Winthrop College
Rock Hill, South Carolina 29733

ASPECTS OF THE BIOLOGY OF THE AUSTRALASIAN HARRIER (*CIRCUS AERUGINOSUS APPROXIMANS* PEALE 1848)

Abstract

The study is based on 18 months of intensive fieldwork on the southwestern coast of the North Island of New Zealand. During this time 212 Australasian Harriers were trapped, re-trapped, measured, sexed, aged, individually marked, and observed. Fortnightly observations of the individually marked population were made over a further seven months. The Australasian Harrier and European Marsh Harrier are considered to be conspecific. Evidence is presented showing that there is no valid reason for considering *Circus aeruginosus* of the Pacific Islands to be a different subspecies from *C. aeruginosus* of Australia and New Zealand. During the breeding season ten terri-

tries in the 12 km² study area averaged 31 ha, nest sites averaged 910 m apart, pairs' overlapping home ranges averaged 9 km², and favourite hunting areas 3 km². A high population density of one bird per 50 ha was calculated. A low fledging success rate of 1.8 young per successful pair and 1.1 young per nest site and two cases of polygyny were recorded during two breeding seasons. Territorial and courtship behaviour, nest parameters, and the parental division of labour are described. Seasonal movements and the dispersion of age and sex classes from the study area at the end of the breeding season are described. Most (66.7%) individually marked adults returned after the autumn dispersal phase and established winter home ranges averaging 9 km². The home range of an adult female in open farmland was calculated to be 14 km² using radiotelemetry techniques. A nonbreeding season population density of one bird per 80 ha was calculated. Communal roosting, which occurred throughout the year, is discussed. Four hundred and seventy food items were identified in the diet from pellets, prey remains, stomach contents, and field observations. In descending order of numerical importance in the diet were mammals (46.4%), introduced passerines (29.0%), insects (7.6%), game birds (6.7%), birds' eggs (4.8%), and aquatic prey (4.6%). Australasian Harriers ate significantly greater numbers of live prey than carrion annually. Adults took significantly greater numbers of agile food items than juveniles. Females ate significantly more large (>200 g) and fewer agile food items than did males. Seven search techniques and five attack techniques, including some buteonine techniques, are identified and described in the Australasian Harriers' wide range of hunting techniques. Ninety-five attacks on prey are recorded, and 15.8% of them were successful. Adults were significantly more successful hunters than juveniles. Cooperative hunting, hunting in the daily cycle, feeding behaviour at carrion, interspecific competition for carrion, interspecific disruption of hunting, and prey escape tactics are described. From a computer analysis of hunting behaviour data it is concluded that adult males are more maneuverable and less conspicuous than adult females and juveniles because they flew significantly lower and faster. Adult males also hunted, to a significantly greater degree, those habitats where there were greater numbers of agile prey. The hunting inexperience of juveniles was quantified. The Australasian Harrier is moderately sexually dimorphic. Current hypotheses proposed to explain the degree of sexual dimorphism in raptors and why the females of most raptor species are larger than males are critically reviewed.

Baker-Gabb, David J. 1978. Aspects of the biology of the Australasian Harrier (*Circus aeruginosus approximans* Peale 1848). M.Sc. thesis, Massey University, Palmerston North, New Zealand. 221 pp.

Present address: Zoology Department
Monash University, Clayton
Victoria 3168, Australia.

BEHAVIORAL AND PREDATORY DYNAMICS OF AMERICAN KESTRELS WINTERING IN THE ARCATA BOTTOMS

A field study of American Kestrels (*Falco sparverius*) was conducted in the Arcata Bottoms, Humboldt County, California, during the winters of 1972-73 and 1973-74,

to evaluate the influence of season, chronological hour, and environmental conditions on time and activity budgets, predatory efficiency, and prey capture.

Data were collected on the behavior of individual Kestrels observed from dawn to dusk. All behavioral acts were recorded with respect to time of day and elapsed time. Special attention was given to their predatory behavior (e.g., mode of hunting, predatory success, prey species captured, and food consumption).

In addition to intensive observation of the behavior of Kestrels, monthly road censuses were conducted in the Arcata Bottoms to obtain density indices of wintering raptor populations. During each field season, densities of small mammal prey species were estimated by periodic trapping in areas Kestrels commonly hunted.

Kestrels were 45.4 percent successful at capturing prey on 635 attempts in 1972-73; of the prey captured, 32 (11.1 percent) were vertebrates and 257 (88.9 percent) were invertebrates. In 1973-74, Kestrels were 60.7 percent successful on 1,198 attempts; of the prey captured, 46 (3.8 percent) were vertebrates and 1,167 (96.2 percent) were invertebrates. The decrease in the percentage of vertebrates captured in 1973-74 compared to 1972-73 corresponded with a drastic reduction in abundance of small mammals. The increase in predatory efficiency during 1973-74, reflected the greater efficiency of Kestrels in capturing invertebrates over that of capturing vertebrates.

The modes of hunting used by Kestrels were perch-hunting, hover-hunting, and flight-hunting. In both years, perch-hunting was most efficient, 51.8 percent and 66.9 percent, respectively; followed by flight-hunting, 23.3 percent and 48.8 percent, respectively; and hover-hunting, 23.8 percent and 26.9 percent, respectively. The predatory efficiency of each mode of hunting was inversely related to the proportion of vertebrate prey captured.

Caching behavior by American Kestrels is described. In 1972-73, 20 acts of prey caching behavior were observed; of these, 11 involved food storage and 9 involved food retrieval. Unsuccessful attempts to retrieve prey were observed 6 times in 1972-73. In 1973-74, 59 acts of prey caching behavior were observed; of these, 36 involved food storage and 23 involved food retrieval. Six unsuccessful attempts to retrieve prey were witnessed in 1973-74. The relative proportion of prey species involved in caching behavior corresponded directly to the relative proportions captured. In 1972-73, 16 (88.9 percent) of the prey items cached were small mammals, and 1973-74, 28 (63.6 percent) were frogs.

The relevance of this study to the functional and numerical components of predation; a comparative analysis of the interrelationships among predatory efficiency, hunting strategies, and taxons of prey; the relevance of time and activity budgets, body size, and foraging strategies to energy economy are discussed.

Collopy, M. W. 1975. Behavioral and predatory dynamics of American Kestrels wintering in the Arcata Bottoms. M.S. thesis. Humboldt State University, Arcata, California. xiv + 211 pp.

Present address: School of Natural Resources
University of Michigan
Ann Arbor, MI 48104